THE ROLE OF THE ANTENNÆ IN THE ORIENTATION OF CARRION BEETLES TO ODORS

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INTRODUCTION

It is now clear beyond reasonable doubt that the principal site of olfactory receptors in the majority of insects is on the antennæ (Marshall, 1935). There is also an increasing number of indications pointing to the existence of auxiliary olfactory receptors on the palpi (Wigglesworth, 1939). Furthermore, it appears that the ability to perceive odors emanating from a distance resides in the antennæ while the palpal end-organs are relegated to the perception of odors from sources near at hand. There is convincing evidence that this is certainly the case in dung and carrion beetles. Warnke (1931) has demonstrated that species of *Geotrupes* require the presence of the apical lamellæ of the antennæ to orient successfully to dung from distances as great as 2 or 3 meters. In the absence of the antennæ these beetles are able to locate dung from a distance of a few centimeters only, and then, provided the palpi have not been removed.

Warnke's experiments were conducted for the most part indoors and involved relatively short distances. The experiments reported below were designed (1) to supply data relative to the mechanism of orientation to carrion in the field under conditions involving maximum distances and (2) to compare the receptors, involved in long range olfactory orientation, of several species of carrion beetles of the family Silphidæ with those of *Geotrupes*, a member of the Scarabæidæ. Since preliminary experiments designed to test the function of the palpi confirm Warnke's work in every respect; this phase is not reported at great length.

MATERIALS AND METHODS

Four stations were established in a northern New England conifer forest. Stations 1, 2, and 3 were equidistant ($\frac{1}{4}$ mile)

from each other. Station 4 was located 300 feet from station 3. At each station the fresh carcass of a red squirrel (*Tamiasciurus hudsonicus loquax*) was hung five feet from the ground in a tree. This procedure was adopted because by forcing beetles to fly to the carcass it reduced the chances of accidental discovery so frequently a feature of orientation to buried carrion. Moreover, the carcass retained its attractiveness over a longer period of time, and each beetle could be captured with a minimum of disturbance to its fellows. Beetles usually began arriving the second day and continued to arrive for a period of 15 days. At this point the carcass was more or less completely cleaned and no longer attracted insects.

Each morning all new arrivals were collected, operated upon, marked with a spot of paint on the pronotum, and liberated at a minimum distance of 15 feet from the base of the tree in which the carcass hung. Operations involved amputation of one or both antennæ at the scape or removal of various numbers of apical segments as outlined in Table II. No anesthetic was used. Captures of returned beetles were made at irregular intervals during the day. All those recaptured were retained for microscopic examination.

In this manner the orientation to carrion of 314 *Necrophorus*, 75 *Silpha noveboracensis* Forst., and 30 *Silpha americana* L. was studied.

THE ROLE OF THE ANTENNÆ

From the results tabulated in Table I it is strikingly apparent that the antennæ are in some manner involved in orientation to odors from a distance. Not a single beetle of the 142 from which each antenna had been severed at the scape returned whereas 60.6 per cent of those lacking one entire antenna were recaptured.

Observations of the reactions of beetles lacking both antennæ did not reveal any immediately apparent abnormality of behavior. It is especially significant that specimens with bilateral amputation were capable of normal flight a few minutes subsequent to the operation. None of the erratic behavior usually associated with antennectomy was observed. In caged specimens neither longevity nor ability to reproduce was impaired. A further indication that bilateral injury of the antennal nerve is not a major

TABLE I

EFFECTS OF PARTIAL AND COMPLETE ANTENNECTOMY ON THE ABILITY OF CARRION BEETLES TO ORIENT TO ODORS FROM A MINIMUM DISTANCE OF FIFTEEN FEET

Species	Lacking 1 antenna		Lacking both antennæ		Lacking tips of antennæ		Controls	
	No. liberated	Per cent returned	No. liberated	Per cent returned	No. liberated	Per cent returned	No. liberated	Per cent returned
Necrophorus tomentosus Weber ..... *vespilloides* Hbst.	78	59.0	110	0	56	27.0	70	87.5
Silpha noveboracensis Forst.	13	61.5	21	0	21	50.0	20	85.0
Silpha americana L.	8	75.0	11	0	6	33.3	5	80.0
Total	99	60.6	142	0	83	32.5	95	85.2

factor preventing normal activity and orientation is seen in the results of experiments in which one or more apical segments of both antennæ of 83 beetles were amputated. Thirty-two and one-half per cent of this group were recaptured. As will be shown below, the relatively low percentage of returns in this category resulted from the fact that tips were cut at different segmental levels without regard to the minimum number of segments required for orientation.

From these observations it appears that the inability of beetles lacking both antennæ to orient to odors is due neither to impairment of normal activity nor to interference with flight functions but rather to the loss of receptors essential to the perception of odors emanating from a distant source.

On the other hand, beetles lacking both antennæ are still able to locate buried carrion from distances of a few (in this case 30) inches. It was on the basis of this type of experiment that Abbott (1927, 1927a, 1936, 1937) concluded that the antennæ of *Necrophorus americanus* (Oliv.), *N. orbicollis* (Say), *N. tomentosus* (Weber), *Silpha inæqualis* Fabr., and *Trirhabda canadensis* (Kby.) are of little importance in orientation to odors and that the olfactory sense is widely scattered over the body. From similar experiments employing animals from which the palpi alone had been removed he concluded that the palpi did not bear olfactory receptors. Unfortunately beetles lacking both antennæ and palpi were not tested. When this is done beetles are no longer able to locate buried carrion. In these respects the Silphidæ are like the Scarabæidæ. Warnke (1931) has shown this to be the case with *Geotrupes* which possess on the antennæ olfactory receptors suited to long range perception and on the palpi auxiliary receptors suited to short range perception. The experiments reported here confirm Warnke's results and indicate that comparable situations exist in Scarabæidæ and Silphidæ.

It is probable that the chief difference between long range and short range perception involves either the thresholds of individual sensilla or a total intensity of stimulation associated with the population density of receptors.

LOCALIZATION OF OLFACTORY RECEPTORS

Because operations involving the removal of individual segments of the flagellum were conducted under field conditions it

was necessary to check microscopically the extent of injury on each beetle after it was recaptured. The results of this post-experimental examination (Table II) show that the presence of

TABLE II

Analysis of the Extent of Antennal Amputation on Recaptured Beetles

Number of beetles	Number of segments of flagellum removed	
	Right antenna	Left antenna
3	1	1
3	1	3
3	1	4
2	2	2
3	2	3
13	2	10

a minimum of one lamella (the apical three segments forming the club of each antenna) is essential to distance orientation. No insect returned which lacked the apical three segments of each antenna although 13 specimens lacking one entire antenna as well as two lamella from the remaining antenna were recovered.

These findings are in complete agreement with the conclusions of Warnke. It is thus apparent that members of the Silphidæ as well as of the Scarabæidæ possess in the apical three segments of the flagellum receptors which are essential to orientation to odors from a distance.

ANTENNAL SENSE ORGANS

Examination of the lamellæ of the four species studied reveals a picture comparable in most respects to that existing in *Geotrupes*. Reference to Fig. 1 shows that the lamellæ in contrast to the other antennal segments possess several hundred sensilla.

Four forms are found here:

(1) thick walled hairs (sensilla trichodea)
(2) thin walled hairs of various lengths (the sensilla chætica of Warnke)
(3) short curved sensilla trichodea (the *gebogene Haare* of Warnke)
(4) thin walled tapering cones (sensilla basiconica).

By contrast the remaining segments of the antenna are remarkably free of sensilla. The same three basic types are found here

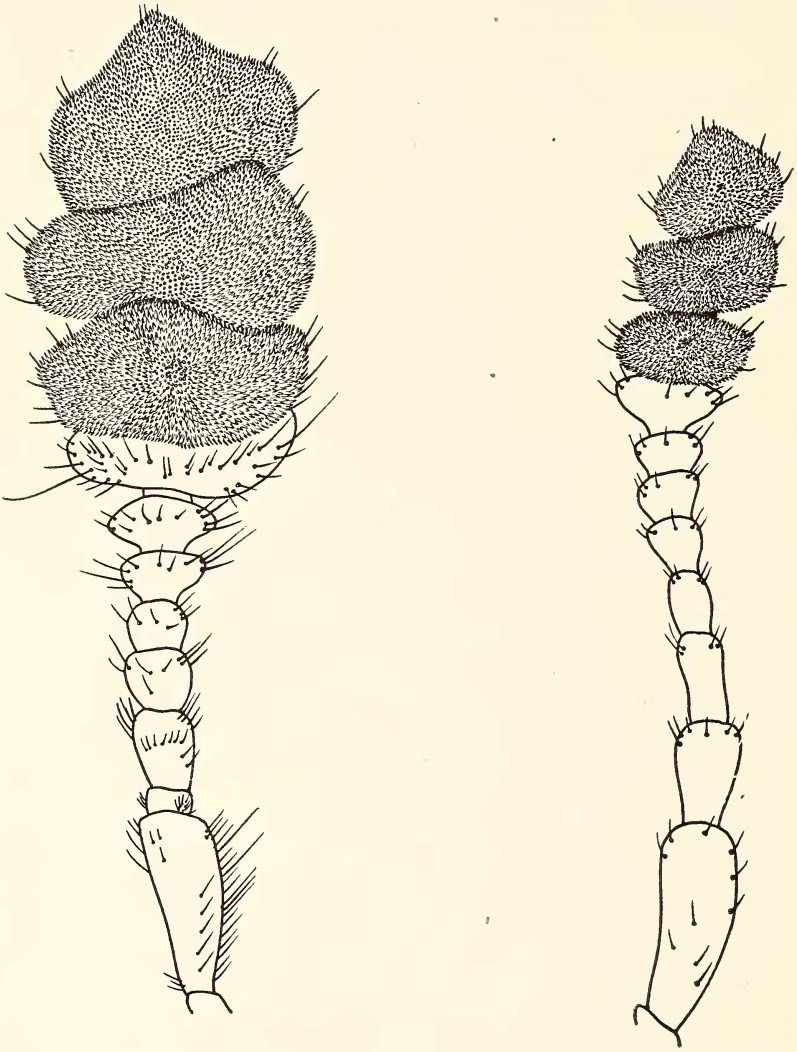

FIG. 1. Dorsal view of an antenna of *Necrophorus tomentosus* Weber (left) and of *Silpha noveboracensis* Forst., (right) showing the distribution of sensilla.

as in *Geotrupes:* thick walled sensilla trichodea, thin-walled hairs of various lengths, and a few sensilla cœloconica. The outstand-

ing difference in the sensory complement of the lamellæ as contrasted with the rest of the antenna is the presence in the former of thousands of short curved sensilla trichodea and delicate sensilla basiconica (Sinneskegel). It would seem, therefore, that one or both of these types subserve an olfactory function. Structurally the latter appear more suited to the task.

MECHANISM OF ORIENTATION

Since there is obviously a limit to the distance over which an odor is effective, it is apparent that dung and carrion beetles cruise more or less at random through the forest until they encounter the periphery of a center of odor diffusion or currents of odor-bearing air. The distance over which the odor is operative depends naturally upon many variables of which the most important is air movement. Under favorable conditions orientation is speedily accomplished. Marked beetles liberated in the foregoing experiments frequently relocated the carrion from a distance of 30 feet in a matter of 15 minutes. A major portion of this time was taken with aimless wandering prior to flight. It is of particular interest that marked beetles liberated 15 feet to the windward of station 3 were frequently recaptured at station 4 some 300 feet distant.

Observations of returning beetles revealed that several flew in from distances of the order of 50 feet in a more or less wavering path and landed either on the trunk of the tree bearing the carcass or on that of a neighboring tree five to six feet away. From this point, after waving the antennæ and extending the lamellæ, the beetle usually flew directly to the carcass.

The speed with which the insect is able to return to the source of an odor from distances in excess of 15 feet and the high percentage of returns from those liberated at this distance points to the existence of a klino-kinetic mechanism rather than truly random movement. As Fraenkel and Gunn (1940) point out, in the confines of a laboratory the chance of locating bait by purely random movement is great. Under the conditions of these experiments the chances are greatly reduced.

The behavior of beetles with only one antenna was remarkably similar. No pronounced tendency toward circus movements was

observed. Animals which landed on the trunks of adjoining trees behaved in every respect like the controls, *i.e.*, the antenna was moved about and the lamellæ extended after which the animal flew directly to the carcass.

It would thus appear that as the gradient becomes steeper the insect is able to orient by means of a klino-tactic mechanism. Circus movements as reported for *Geotrupes* following unilateral extirpation were not observed here although it is not improbable that they may have been less pronounced in flight and consequently overlooked.

SUMMARY

The orientation of the following species of Silphidæ to odors in the field under conditions involving maximum distances was studied: *Necrophorus tomentosus* Weber, *N. vespilloides* Hbst., *Silpha noveboracensis* Forst., and *S. americana* L.

Experiments involving various combinations of complete and partial antennectomy and palpectomy indicated that the principal site of olfactory receptors is on the antennæ and that auxiliary olfactory receptors are located on the palpi. The former are suited to long range perception; the latter, to short range perception.

Antennal olfactory receptors are confined to the apical three segments or lamellæ. These segments possess special sensilla trichodea and sensilla basiconica not found elsewhere on the antenna. The sensilla basiconica are probably olfactory end-organs.

At extreme distances orientation to odors is probably by means of a klino-kinetic mechanism. As the gradient becomes steeper the insect is able to orient by means of klino-taxis. Circus movements following unilateral antennal extirpation were not observed.

With respect to the rôle of the antennæ in orientation to odors from a distance the Silphidæ studied are similar to *Geotrupes* (Scarabæidæ).

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